Gorilla Biology

A Multidisciplinary Perspective

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Ryder, O.A., Garner, K.J., and Burrows, W. (1999). Non-invasive molecular genetic studies of gorillas: Evolutionary and systematic implications. *American Journal of Physical Anthropology, Supplement* **28**, 238.

Tuttle, R.H. (1998). Global primatology in a new millennium. *International Journal of Primatology*, **19**, 1–12.

Uchida, A. (1996). What we don't know about great ape variation. *Trends in Ecology and Evolution*, **11**, 163–168.

2 *A history of gorilla taxonomy*

COLIN P. GROVES

Prologue

In the fifth century BC the Carthaginian admiral Hanno was commissioned to sail down the west coast of Africa and found Carthaginian colonies. After dropping off colonists at intervals, he sailed on, and eventually came to a fiery mountain, near which was a bay in which was an island. In the island was a lake, and within this another island, full of savage hairy people whom the interpreters called "gorillas". The Carthaginians tried to catch them; the men escaped and threw stones from the cliffs; but they caught three women and, finding them untameable, killed them, skinned them and took their skins back to Carthage.

Hanno's voyage has been endlessly discussed: did he get to Cameroon? – to Sierra Leone? – just to southern Morocco? Were they really gorillas? – or chimpanzees? – or baboons? – or even Neandertalers? What language was this word "gorillas", and who were these interpreters?

Heuvelmans (1981) was the first to point out what should have been obvious: the account of the voyage which has come down to us is in Greek, not Punic (the language of Carthage), and it was written some centuries after the voyage was said to have taken place. In the interval, who knows how much it has been embellished, abbreviated, and perhaps modified to accord with various accounts of Greek, Phoenician and Egyptian ocean voyages? There seems little hope of ever establishing what those so mercilessly slaughtered "gorillas" actually were, or where they lived. Rightly or wrongly, they live on – in their name.

Real gorillas entered European literature for the first time in an account by Andrew Battell, an English sailor held prisoner by the Portuguese in Angola (almost certainly Cabinda, the enclave north of the Congo River mouth), in the sixteenth century. In his account of the region, he wrote of two human-like "monsters", Pongo and Engeco. Though mixed up with all kinds of misinformation, the description of Pongo is certainly that of a gorilla. Alas, by the late eighteenth century most Great Apes had become inextricably confused under the term "orangutan", with the result that *Pongo* became the generic name for the great red ape of Borneo and Sumatra!

The gorilla becomes known to science

The first scientific description of the gorilla, with its scientific name *Troglodytes gorilla*, was published without fanfare, without fuss of any kind, by Dr. Jeffries Wyman, an anatomist of Boston. Wyman, however, was not the author of the name. The *Proceedings of the Boston Society of Natural History* states that "Dr. J. Wyman read a communication from Dr. Thomas S. Savage, describing the external character and habits of a new species of *Troglodytes* (*T. gorilla*, Savage) recently discovered by Dr. S. in Empongwe, near the river Gaboon, Africa"; this is followed by Dr. Savage's communication, presumably a letter, then a note that Dr. Wyman exhibited some bones, and what seems to be a transcript of Wyman's description of them including the differences from the chimpanzee.

The *International Code of Zoological Nomenclature* (4th edition) states quite clearly, in Art. 50.2:

> **Names in reports of meetings.** If the name of a taxon is made available by publication of the minutes of a meeting, or an account of a meeting, the person responsible for the name, not the Secretary or other reporter of the meeting, is the author of the name.

Therefore the author of the name *T[roglodytes] gorilla* is Savage, not "Savage and Wyman" as commonly cited.

It should be explained that, at that time, the generic name in common use for the chimpanzee was *Troglodytes* (E. Geoffroy St. Hilaire, 1812). It is now realized that this name is preoccupied (i.e., the name had already been proposed for another animal); so the name *Troglodytes* Vieillot, 1806, is the generic name of the wren, and after much struggle we have settled down with *Pan* Oken, 1816, for the chimpanzee.

In December of the same year a fuller description appeared (Savage and Wyman, 1847). Savage gave a full account of its discovery, giving the type locality (the mission house where he had been given the skeletal remains and told of its external appearance and habits) as the Gaboon River, at 0°15′ N, quoting Hanno and Battell, and explaining that he had adopted Hanno's term as the specific name; followed by an even more detailed account of its osteology by Wyman. Nonetheless the earlier paper, in August of that year, stands as the original description of the name.

Early in the following year Owen (1848*a*) described further specimens, supplied to him by Savage, under the name *Troglodytes savagei*; later (Owen, 1848*b*) he admitted priority to the name given by Savage himself. The specimens brought to the U.S.A. by the Reverend Savage are today in the Museum of Comparative Zoology, Harvard. Those described by Owen are in the Natural History Museum (formerly British Museum (Natural History)), London.

It was not long before the gorilla was awarded a genus of its own. Isidore Geoffroy St. Hilaire (1852), the son of Etienne who had given the chimpanzee its earliest, if already preoccupied, generic name (*Troglodytes*), set it apart in a new genus, *Gorilla*.

Several species of gorillas? Nineteenth-century thoughts on the matter

No sooner had he accorded the gorilla its own genus, than Isidore Geoffroy received a skull which differed so markedly from those he had previously seen that, though it likewise came from Gabon, he felt sure that it represented a second species: *Gorilla gina* (I. Geoffroy St. Hilaire, 1855). Early in the next decade Slack (1862) described a third species, *Gorilla castaneiceps*, based on the coloured cast of a head in which the crown hair was red, not black. We now know, of course, that the colour of the crown is polymorphic in gorilla populations. The cast studied by Slack is still in the Academy of Natural Sciences, Philadelphia; ironically, when I saw it, it had been repainted – completely black.

More enduring was the name given by Alix and Bouvier (1877) to a supposed dwarf gorilla, *Gorilla mayema*. The small female gorilla on which this name was based differed from *Gorilla gorilla* in osteological details and in its pelage, most notably in having a "collar" of hair round the face and the back covered with long, thick hair. The type locality was given as the village of King Mayêma, on the banks of the Quilo at 4° 35′ S, but was later changed by Famelart (1883), on what evidence we do not know, to Conde, near Landana.

Elliot (1913) could not find Alix and Bouvier's specimen when he searched for it in the Muséum National d'Histoire Naturelle, Paris. I found a female skull in the Laboratoire d'Anatomie Comparée of the Museum, which I judged might have been the type of *G. mayema*; it is the smallest adult gorilla skull I have seen.

In the last years of the century an enormous gorilla, said to be 207 cm long (how measured?!) and with a span of 280 cm, was shot, in the uncompassionate way of those days, by H. Paschen at Yaounde, Cameroon, and figured and named *Gorilla gigas* by the notorious Ernst Haeckel in 1903.

Early studies on the gorilla's anatomy

The type and follow-up descriptions of the gorilla (Wyman, 1847; Savage and Wyman, 1847) themselves contained detailed descriptions of the gorilla's osteology. Further detailed descriptions were given by Owen (1848*a*,*b*,*c*, 1862*a*,*b*).

By the time Owen was writing his second series of papers, in the 1860s, the Darwinian controversy was in full swing, and Owen was especially anxious to use his studies of the gorilla and other apes to combat "the hypothesis of transmutation". Already (Owen, 1857) he had made it clear that, for him, characters of the brain set humans clearly apart from other mammals, as sole representatives of a new subclass, Archencephala. Only the human brain, he claimed, had a special posterior lobe of the cerebrum, covering the cerebellum; had a posterior horn of the lateral ventricle; and had a hippocampus minor. He repeated these assertions in several other places (see, for example, Owen, 1861), despite their accuracy being increasingly challenged by Huxley. It was the examination of a gorilla brain that led Huxley (1867) to contradict Owen fully and finally, and show that "Man" was far from unique in those features: Owen had been caught letting his prejudices get in the way of his objectivity, and the Darwinian revolution became that much more firmly entrenched. The whole story, of the irrational behavior and downright dishonesty displayed by this great anatomist, is much more complicated (and shaming to Owen) than I have given here; it has been most recently recounted by Wilson (1996).

Subsequent descriptions of the anatomy of the gorilla (Bischoff, 1880; Sonntag, 1924) were much more simply factual. Others (Hartmann, 1886; Keith, 1896; Duckworth, 1915) were more concerned to place the gorilla in evolutionary context, but were equally objective and no one has questioned their accuracy. Small packets of new information were constantly fed into the system as well; thus Neuville (1916) described some skulls of adult males which, unexpectedly, lacked any sagittal crest (and later (Neuville, 1932), in view of the taxonomic prolixity that was to follow, was able to congratulate himself for not having burdened gorilla taxonomy with a new species name for them!).

Paul Matschie: Let a hundred species bloom

Professor Paul Matschie was an anti-evolutionist, with in addition some highly bizarre ideas about mammalian taxonomy and variability; though quite untrained, he had been appointed curator of mammals in the Berlin Museum. Representatives of each group of animals from each river valley simply had to be different species; it was just a matter of finding the differences. Uncounted scores, perhaps hundreds, of new mammal species were launched into a brief existence under this philosophy; on several occasions a buffalo or antelope would even be described as two separate species (represented by the left and right sides of the animal!) because, being shot on watersheds, they were interpreted as hybrids! Until his eccentricities became so outrageous that they could no longer be ignored, Matschie bestrode mammalian taxonomy for the first quarter of the twentieth century, and his contemporaries could only look on in admiration and try to emulate him.

Two of Matschie's admirers stand out in the present context. The Hon. Walter Rothschild was a millionaire who was passionately interested in natural history, and founded his own private museum for its study, at Tring, north of London. Daniel Giraud Elliot was a general zoologist who worked first in European museums, then in Chicago, and "retired" to an honorary post in the American Museum of Natural History, New York, and in his retirement studied primates, not entirely to the betterment of our understanding. Among them Matschie, Rothschild and Elliot increased the number of putative gorilla species and subspecies nearly fivefold.

As if by accident, the first of the many new gorilla taxa that Matschie described was a good one: the mountain gorilla, *Gorilla beringei* (Matschie, 1903). Captain von Beringe had shot two gorillas at 3000 m on Mt. Sabinio in the Virunga mountains; these differed from *Gorilla gorilla* in their thicker pelage and much stronger beard, and the skull of the male differed from 25 available skulls of *G. gorilla* in several respects:

- narrower, more pointed nasal bones
- palate longer than the distance from its posterior end to the foramen magnum, instead of shorter as in *G. gorilla*
- weaker supraorbital torus, only 8–9 mm thick (cf. more than 11 mm)
- lack of the spur or crest which in West African skulls extends from the lower orbital margin to the infraorbital foramen.

"Ich nenne ihn *Gorilla beringeri*", wrote Matschie (1903:257). As the collector's name was von Beringe, and Matschie himself knew this, this form of the name clearly ranks as an Incorrect Original Spelling under Art. 32.5 of the *Code*, and must be corrected (to *beringei*) while retaining the original author and date (Matschie, 1903). I might add that, of the four skull characters, only the long palate is a good, consistent difference between *G. gorilla* and *G. beringei*.

The type specimen of *G. beringei* could not be discovered when I visited the Zoologisches Museum A. Humboldt in Berlin in the 1960s.

The following year Matschie revised the genus *Gorilla*, recognizing four species: *G. gorilla*, *G. castaneiceps* (with *G. mayema* a synonym), *G. beringeri* (still spelled incorrectly) and a new species, *G. diehli*, from Dakbe (type locality), Oboni and Basho, on the Cross River in the then-German territory of West Kamerun (Matschie, 1904). The striking difference between *G. diehli* and other gorillas was in the broad, low nuchal surface. Of nine skulls collected by Herr Diehl – most of them from African huts, where they were kept as "fetishes" – eight were of the new species, but one, a female from Basho, differed in no respect from Gabon and southern Cameroon gorillas, and Matschie consequently

referred it to *G. gorilla*. All the Cross River skulls are still in the Museum in Berlin.

Rothschild, meanwhile, purchased the Paschen gorilla from the Hamburg Museum for 20 000 marks for his own museum and, apparently unaware that Haeckel had already awarded it a name, described it as *Gorilla gorilla matschiei* (Rothschild, 1905:415). Comparing its skull with four large skulls of the Gabon gorilla, he drew attention to differences in the shape of "the hinder surface of the head", the basioccipital bone, and the condyle and coronoid of the mandible; he did not specify exactly what these differences would be, but from his comparative table the nuchal surface would be longer and wider, and the basioccipital shorter. Rothschild reduced *diehli* to the status of subspecies under *G. gorilla*, and regarded Slack's *castaneiceps* as a mere "casual aberration" of the Gabon gorilla. It must also be stated that Rothschild was actually one of the pioneers of the subspecies concept, and argued very forcibly (1905:439–440) for the trinomial.

The Rothschild Museum, Tring, was incorporated into the then British Museum (Natural History) in 1939, and the type skull of *G. g. matschiei* is now in the Mammal Section of the Natural History Museum; but, the last time I looked, its mounted skin was still on display in Tring.

Matschie (1905) described his third new species, *Gorilla jacobi*, from Lobomouth, on the Dja River, in southern Cameroon. The type skull and the other two skulls are still in Berlin. The distinguishing characters are simple individual variation; but it is worth recording that the type is the largest gorilla skull I have seen.

Matschie was also held responsible for the description of *Gorilla gorilla schwarzi* by Fritze (1912), from "Sogemafarm" (correctly Sogemafam) in southwestern Cameroon, but there is no provision in the *Code* (see especially Art. 50) that anyone but Fritze should be cited as the author of the name. I could not find the type of this supposed subspecies in the Karlsruhe museum. 1913 saw the publication of Elliot's epoch-making, much-maligned *Review of the Primates*. He evidently did not know of *schwarzi*, but he recognized (with admittedly some misgivings) all the taxa that had been described up till then: *gorilla, matschiei, diehli, jacobi, castaneiceps, beringei, mayema* (but added a special touch of his own as far as the last was concerned), and two which he did not name, leaving that task to Matschie. Matschie (1914) took up the challenge, naming the two which Elliot had signalled: *Gorilla hansmeyeri*, from south of the Dume River, on the Assobam road between Mensima and Bimba; and *Gorilla zenkeri*, from Mbiawe on the River Lokundje, six hours upriver from Bipindi (both in southern Cameroon). He also named a second eastern species, *Gorilla graueri*, from 80 km northwest of Boko, on the western shore of Lake Tanganyika, in the present-day Democratic Republic of Congo, formerly Zaïre, and noted its similarity to *G. beringei* (which by this time he was spelling correctly). The types of these three putative species are still in the Berlin museum.

This was Matschie's last paper on gorillas. He had described six supposed new species/subspecies, had been possibly responsible for a seventh, and had had one named after him. His ideas became more and more mystical; eventually he concluded that species' distributions were bounded not by watersheds but by the diagonals of the even degrees of longitude and latitude. He died in 1926, aged only 64.

Only four other species and subspecies of gorillas – if we exclude Frechkop's contribution (below) – were described. Lönnberg (1917), under the impression that mountain gorillas in the Virunga range were confined to individual volcanoes, described *Gorilla beringei mikenensis* from Mt. Mikeno (Matschie's *beringei* was from Mt. Sabinio). Rothschild (1927) described *Gorilla gorilla halli* from Punta Mbouda (correctly Mbonda) in Equatorial Guinea. Finally Schwarz (1927) described another eastern form, *Gorilla gorilla rex-pygmaeorum* from Luofu, west of Lake Edward; whatever one thinks of his taxonomic assessment, he certainly had poetry in his soul (the name means "king of the pygmies"); and in the same paper he mentioned and briefly described three skulls from Djabbir, near Bondo, in the Uelle valley, with a footnote: "Note du Dr. Schouteden: ils s'agit du *G. uellensis* Matschie" (according to the *Code*, Schouteden must be regarded as author of this name). The types of all these taxa are still extant (*mikenensis* in Stockholm, *halli* in London, the other two in the Museum voor Middenafrika, Tervuren, Belgium).

Pygmy gorillas?

Alix and Bouvier's supposed pygmy gorilla, *Gorilla mayema*, has refused to lie down, almost up to the present day. In his 1905 paper Rothschild indicated that he believed *Gorilla manyema* (*sic!*) to be actually a chimpanzee, but three years later (Rothschild, 1908) he stated that he had received specimens of *Gorilla manyema*, and now saw that it was not a chimpanzee after all but must be the gorilla race of the "South Congo". The skull, he said, is narrow; and a photograph of the whole animal showed, he said, "very sharply defined pale and dark areas".

Now, Manyema (now spelled Maniema) is a district in Democratic Republic of Congo, east of the Lualaba River, where eastern lowland gorillas are found. Did Rothschild misspell *mayema* as *manyema* because that was the source of his specimens, and by "South Congo" did he mean Upper Congo? One of the Rothschild Collection skulls in the Natural History Museum, BM 1939.945,

an old male, has "*G. g. manyema*. Upper Congo" written on it, and assorts as an eastern lowland gorilla. In my first publication on gorillas (Groves, 1967), I used the name *manyema* for the eastern lowland gorilla; but Corbet (1967) pointed out that, whatever the circumstances, *manyema* is clearly an inadvertent error for *mayema* and so has no status in nomenclature. And, of course, Rothschild's misreading of the name certainly dissociated it from pygmy gorillas!

Elliot (1913) searched unsuccessfully for Alix and Bouvier's specimen in Paris, and then applied the name, without giving any justification, to a male, female and young (skulls and mounted skins) from "Upper Congo" in the Senckenberg Museum, Frankfurt. Having the impression that these specimens were intermediate between a gorilla and a chimpanzee, he erected a new genus, *Pseudogorilla*. Compared to *Gorilla*, the genus *Pseudogorilla* could be distinguished by its small size, lack of sagittal and nuchal crests, more rounded forehead, and other features.

In 1943, Frechkop gave it as his opinion that the Frankfurt specimens were not, in fact, the same as Alix and Bouvier's, so he renamed them *Pseudogorilla ellioti*.

Actually, two years after Elliot's book was published, Miller (1915:6, n. 1) revealed the true nature of the specimens: "an immature male with all the teeth in place but with the basal suture open and the temporal ridges separate ... and a mature female with the basal suture closed and the temporal ridges joined." I have seen the specimens, and I concur. Maybe Elliot had never seen subadult male skulls, or even those of adult females; or maybe he had seen them but taken little notice of them. Presumably the skins, mounted and on display to this day in the Senckenberg Museum, belong with the skulls; they are, at any rate, of male and female of corresponding ages (plus an infant). Heuvelmans (1981), inclined to accept the real existence of pygmy gorillas, drew attention to the long, sharp canines visible in the open mouth of the mounted male skin; but the canines are made of wood (Dieter Kock, personal communication).

Throughout the century the ghost of the pygmy gorilla has been periodically resurrected. I hope I have finally laid it to rest (Groves, 1985).

Order out of chaos

Schwarz (1928) was perhaps the first to try to reduce the plethora of described species and subspecies to manageable proportions. He recognized just one species, *Gorilla gorilla*, with the following subspecies:

G. g. gorilla (synonyms *castaneiceps, mayema, halli*)
G. g. matschiei (synonyms *jacobi, schwarzi, hansmeyeri, zenkeri*)
G. g. diehli
G. g. uellensis
G. g. rex-pygmaeorum
G. g. graueri
G. g. beringei (synonym *mikenensis*)

He gave no descriptions of these subspecies, and the "revision" is probably more in the nature of a conveninent disposal – for example, all the southern Cameroon taxa are lumped into one subspecies, the Gabon and Equatorial Guinea taxa into another.

The first major formal revision, which became standard for 40 years, was that of Coolidge (1929). This can be criticized, and it has been (Haddow and Ross, 1951), but probably Coolidge did the best that could be done with the restricted amount of material available to him. Coolidge put all gorillas into one species, as had Schwarz, and recognized only two subspecies: *G. g. gorilla* for all western gorillas, and *G. g. beringei* for all eastern ones. The narrow cranium and long palate of the latter were the most striking differences. He noted that the skulls from Bondo (Schouteden's *uellensis*) were indistinguishable from *G. g. gorilla*, and suggested that they had originated further west and had ended up in the Bondo region by trade, but he later (Coolidge, 1936) acknowledged that the evidence was against this, and that gorillas were (or had been) native to the region.

Schultz (1934) argued that Coolidge had underestimated the differences between western and eastern gorillas, and that they were actually distinct species. He listed 20 differences between them. Looking over his list, some of the differences are cogent, some not, but the major criticism is that for the eastern ("mountain") gorillas only Virunga and Kahuzi specimens were available to him; the skeletal differences related mainly to Virunga, the external differences to Kahuzi, none to any of the other eastern populations. Groves and Stott (1979) tried to determine how far Schultz's features could be applied to other eastern populations – with varying results.

A little-known paper by Rzasnicki (1936) used indices taken from human craniometry to sort out gorillas, using Coolidge's data. He regarded six "complexes" of skull measurements as originating in different parts of the distribution and spreading out to different populations so that, just as it was customary until mid-century to regard different human populations as consisting 40% of one race, 25% of another, 20% of a third, and so on, so it was with gorillas. The three centres-of-origin of these "complexes" which he elucidated were made subspecies: these were the Cross River (*G. g. diehli*), the rest of the western area (*G. g. gorilla*), and the eastern area (*G. g. beringei*).

Vogel (1961) studied mandibles. He separated *G. beringei* as a distinct species from *G. gorilla*, and within it recognized two subspecies: *G. g. beringei*

(Virunga) and *G. g. graueri* (rest of the eastern region). He thus deserves credit as the first person to distinguish the eastern lowland gorilla as a category from the true mountain gorilla, although as pointed out by Schaller (1963) some of his localities for the eastern region are incorrectly identified and, in a study based on 38 jaws (divided, of course, into male and female), any misallocation matters.

The definitive revision that finally took over from Coolidge's and became standard for 30 years was that of Groves (1967). The advantages that had accrued in the interval included more material, from a wider range of localities; better understanding of gorilla ecology and distribution; and, in particular, new analytic methods especially multivariate analysis. I measured and took notes on 469 male and 278 female skulls, and allocated the crania to 19 circumscribed geographic regions and the mandibles (of which there were fewer specimens than of crania) to ten such regions, with at least 11 specimens in each. I took up to 45 measurements on each skull. As it is important as a general statistical rule of thumb that the number of specimens per sample should exceed the number of variables, I ran correlation coefficients and made ten intercorrelated groups of cranial variables and six of mandibular variables; I then selected one from each group and ran a series of Mahalanobis generalized distance analyses.

The results enabled me to pool the 19 cranial and 10 mandibular samples into eight major regions ("demes"), as follows: (a) Western: Coast (and including the whole of Gabon), Cameroon Plateau, Sangha River, and Cross River; (b) Eastern: Utu (i.e., lowlands east of the Lualaba), Tshiaberimu, Itombwe ("Mwenga-Fizi" region of Schaller, 1963), and Virunga. Unallocated specimens were from Bondo (*G. g. uellensis* Schouteden, 1927), Lubutu (north of Utu), Kahuzi, and Kayonza (now preferably called Bwindi-Impenetrable) Forest. All western samples, even when grouped into the four regions, were very close – the Cross River sample somewhat more distinctive than the rest – and I considered them to represent a single subspecies, *Gorilla gorilla gorilla* (Savage and Wyman, 1847, *recte* Savage, 1847); and the Bondo specimens fell well within their range of variability. Among the Eastern regions, however, the Virunga sample fell well away from the others, and I restricted *G. g. beringei* to the Virunga population; the others I grouped into a third subspecies, which at first (Groves, 1967) was called *G. g. manyema* (Rothschild, 1908), but after criticism by Corbet (1967) I called it *G. g. graueri* (Matschie, 1914). The few Kahuzi specimens seemed rather closer to *beringei*, the Bwindi ones to *graueri*.

Groves and Stott (1979) returned to the Kahuzi and Bwindi question; a little new information about them had meanwhile become available. The Kahuzi gorilla was now shown quite clearly to be *graueri*, while the Bwindi gorilla was still equivocal, but perhaps closer to *beringei* after all.

Recent understanding of the anatomy of the gorilla: Normal and pathological

The landmark in anatomy, that brought order out of chaos as Coolidge (1929) had done for taxonomy, was the volume edited by Gregory (1950), the Henry Cushier Raven Memorial Volume, *The Anatomy of the Gorilla*. Featuring papers by some of the leading human and primate anatomists of the mid-century era, S.L. Washburn, H. Elftman, W.B. Atkinson, W.L. Straus and A.H. Schultz, the centerpiece was a profusely illustrated *tour de force* on regional anatomy by the dedicatee himself, H.C. Raven. It is perhaps disappointing that the papers are in the main exclusively descriptive, only Straus and Schultz and to a lesser degree Washburn having much in the way of a comparative approach. But the data were now, for the very first time, laid out in an accessible, detailed form, in a single volume.

The era of gross anatomy was coming to an end. Cave (1959) published a study on the nasal fossa of a gorilla fetus, and later (1961) on the frontal sinus; he confirmed that, like *Pan* and *Homo, Gorilla* has a true frontal sinus of ethmoid origin. Cave had specifically examined frontal sinuses from a phylogenetic point of view, and from now on anatomical studies would be problem-oriented in approach: pathology, function and so on.

The first problem studied by Angst (1967, 1970) was sagittal and nuchal cresting. He confirmed the general view that the nuchal crest and the posterior part of the sagittal crest depend predominantly on jaw length and associated m. temporalis size, whereas the anterior part of the sagittal crest is associated with shorter jaws; but the matter is more complicated than this. For example, two adult male gorilla skulls lacking a sagittal crest had a smaller cranial capacity than any other males. Later the same author (Angst, 1976) published what is probably the most complete survey to date on cranial capacity. In 38 adult males measured by him, cranial capacity averaged 565.2 cm^3, with a range of 440–672 cm^3 (but he noted an unusually large value of 752 cm^3 published by Schultz (1962)); in 27 adult females, 482.6 (403–583) cm^3. These values would seem to be achieved around the time of eruption of the canines and third molars.

Pathology has been another concern of more recent studies. The skulls of gorillas reared in captivity in the pre-war period showed characteristic differences from those obtained from the wild (Angst and Storch, 1967). The pre-war reared gorillas Bobby (Berlin), Gargantua (from a circus) and Bushman (Chicago) had very dorsoventrally low orbits and prominent supraorbital tori. Frequently the incisors are unusually procumbent. Cranial capacity seems to be small. Bobby had a strikingly vertically oriented planum nuchale. The skull of Abraham, who died in Frankfurt Zoo in 1967, was much more "natural" than this, reflecting

favorably on the improvements in captive husbandry that had taken place in the meantime.

Pathology in the wild was studied for mountain gorillas by Lovell (1990). Dental abscesses were frequent, as was antemortem tooth loss, often associated with extensive alveolar bone loss. Lovell discussed this phenomenon and its association with the heavy build-up of calculus; it is not a result of the destruction of interdental alveolar bone by bamboo "packing", as was hypothesized by Colyer (1936). Traumatic injuries were recorded, but the most extensive skeletal pathology was arthritis.

Groves and Humphrey (1973), studying cranial asymmetry, drew attention to the grossly deformed skull of an adult male, found at the foot of Mt. Karissimbi, which was donated by the late Dr. Dian Fossey to this author. The left ascending ramus and mandibular condyle are almost undeveloped, making the whole skull extremely lopsided, perhaps due to destruction in infancy of the left m. temporalis (unsuccessful attempted infanticide?). The only detailed description of extreme skeletal trauma in a western gorilla (from the Sangha River) had been by Maly (1939), who described the results of a severe wound, presumably by a spear, to the pelvis, spinal column and leg bones, and another wound to the skull knocking out the front teeth and damaging part of the upper jaw.

Sarmiento (1994) made a study of the functional anatomy of the hands and feet, documenting in detail for the first time the extent of the gorilla's terrestrial adaptations. Functional anatomy is very much the current concern, and studies like Sarmiento's are clearly the future of the field.

Epilogue

The genetic revolution has done much to revitalize systematics, and has stimulated a great deal of research on interrelationships within the Hominoidea. Meanwhile conservation concern has renewed attention on two outlying populations – Bwindi and the Cross River.

Garner and Ryder (1996) have analyzed a 250-bp sequence from the "hypervariable" region of the D-loop of mitochondrial DNA. They found a large difference between western and eastern gorillas, and a smaller difference between *graueri* and *beringei*; there was no concordance with geographic origin within either western gorillas or mountain gorillas (the latter included both Virunga and Bwindi), but some of the divisions among western gorillas were very deep (implying a demic population structure: Simon Easteal, personal communication). Ruvolo *et al.* (1994) had previously analysed the COII sequences of several hominoids; though their gorilla representation was smaller (only four western, one *graueri*, one *beringei*) they were at any rate able to make comparisons: thus the *graueri* vs. *beringei* difference was the same as the difference between modern human races, and the western vs. eastern difference nearly twice as great (but less than half that between common and pygmy chimpanzees).

Sarmiento *et al.* (1996) have found that, as far as the admittedly limited evidence goes, the Bwindi gorillas fall in many morphological characters beyond or at the edge of the range of those from Virunga. Eventually, they suggest, the Bwindi gorillas will have to be recognized as a separate subspecies. A suggestion was made (Anon., 1996) that this proposal is at odds with the findings of Garner and Ryder (1996) that Virunga and Bwindi mitochondrial lineages are intermixed; an interpretation to which Butynski *et al.* (1996) took exception, pointing out that Ryder himself had commented that there was no necessary conflict.

I might note here that there is an unfortunate tendency to regard genetic data as "the answer"; if morphologically defined subspecies do not appear to be characterized by unique DNA lineages (especially mtDNA), then they are somehow not different, that the evidence of the eyes and the calipers is illusory. Concerning another case of conservation concern (sable antelopes) I wrote:

> Mitochondrial lineage sorting just has not occurred yet among sable subspecies ... which is reasonable when you consider that what is characteristic of subspecies is that they do not have fixed allelic differences between them, unlike species ... Unless we take the phenotypic differences to be merely environmental – due to different conditions of rearing, no more – then the existence of such differences is *ipso facto* evidence that [subspecies] differ genetically. This genetic differentiation does not reside in the control region of mtDNA, that's all: and, as Avise himself, the founder of the phylogeography concept, has shown, lineage sorting is not the same thing as population separation. (Groves, 1998)

Phenotypically, eastern and western gorillas are very different. Their skulls would probably always be distinguishable; certainly externally they are distinct in colour and other characters, such as nose form (Cousins, 1974). It is on this basis that I think that there are, after all, two full species: *Gorilla gorilla* and *Gorilla beringei* (Groves, 2000, 2001). Within the latter, for the moment both recognized subspecies, *G. b. beringei* and *G. b. graueri*, should stand as homogeneous entities, but further enquiry may well establish that the Bwindi population should be separated from *beringei* and one or more of the Utu, Tshiaberimu and Kahuzi populations should be separated from *graueri*.

Among western gorillas, there has been a move to reinvestigate the status of *diehli*, the gorillas of the Cross River (now in Nigeria). Stumpf *et al.* (1998) used size-adjusted cranial data to show that this population differs much more strongly than the raw data of Groves (1967, 1970) had suggested.

I made my craniometric data available to Rebecca Stumpf, who put them on a datafile and kindly sent me a copy. I ran the male skull data on SPSS,

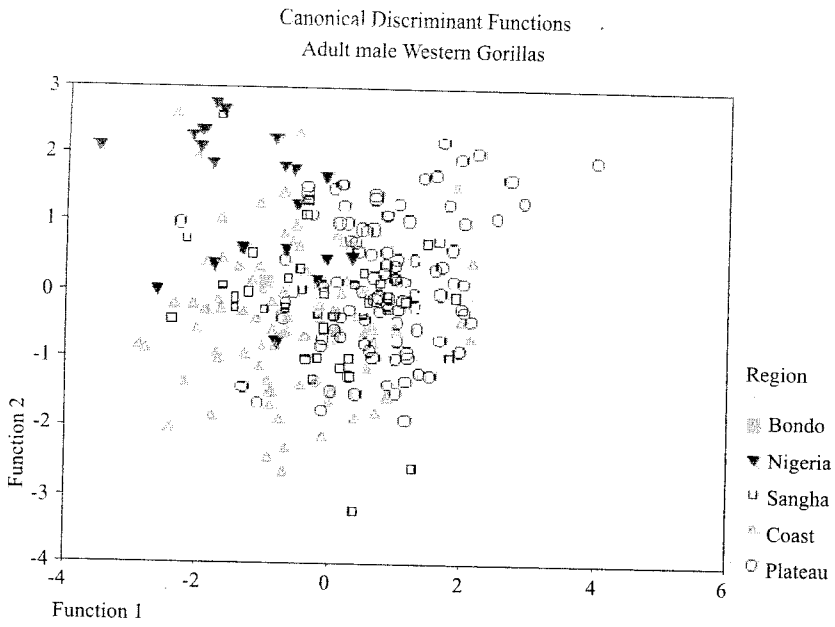

Fig. 2.1. *Gorilla gorilla* male skulls, grouped by major region. The Bondo skull was entered as an unknown. The first discriminant function accounts for 65.0% of the variance, the second for 30.4%. Standardized canonical discriminant function coefficients are as follows:

	Function 1	Function 2
Braincase length	−0.521	0.841
Palatal breadth at M^1	0.298	0.001
Facial height	−0.346	0.346
Interorbital breadth	0.345	−0.062
Breadth of nuchal surface	−0.569	−1.052
Biporionic breadth	0.708	0.628
Basal length	0.228	−0.487
Maximum cranial length	0.328	−0.408
Palatal length	0.400	0.007
Basion to inion	0.159	0.267

Discriminant, just as a preliminary test. In five minutes I recreated the analyses that had taken six months in 1966. As an experiment, I tested the differentiation of the Bwindi population (further data kindly supplied by T. Butynski) and the Cross River sample. The results are shown in Figs. 2.1–2.3.

In Fig. 2.1 we see that the Cross River sample occupies its own cluster, in a way which the other regional groups of *G. g. gorilla* do not – even the single skull from Bondo is buried deep in the general Cameroon/Gabon/Congo scatter. If discriminant analysis of raw data can suggest such a separation, it is evident that size-adjusted data would have much greater potential to reveal the validity of *Gorilla gorilla diehli*.

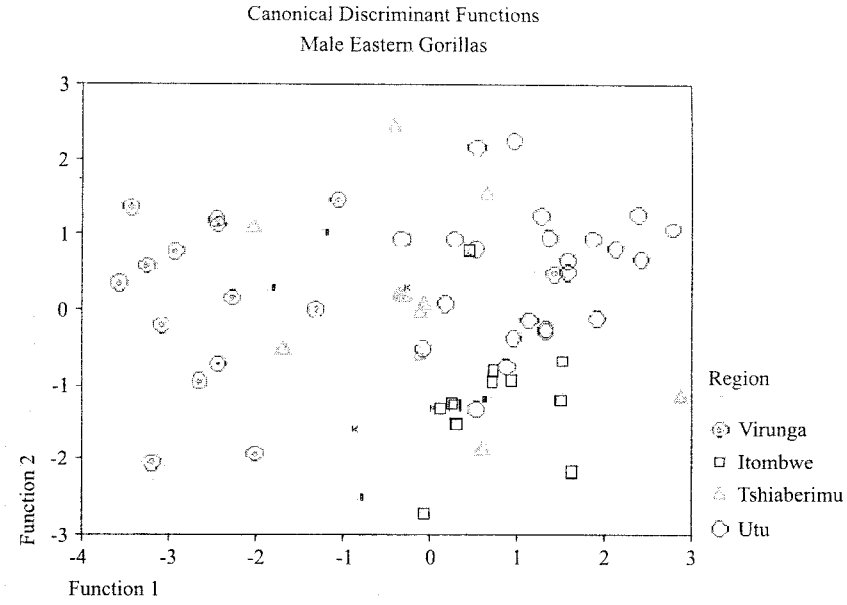

Fig. 2.2. *Gorilla beringei* skulls. Ungrouped cases: B = Bwindi; K = Kahuzi. The first function accounts for 77.0% of the variance, the second for 16.9%. Standardized canonical discriminant function coefficients are as follows:

	Function 1	Function 2
Braincase length	−0.150	−0.278
Palatal breadth at M^1	0.530	0.051
Facial height	0.624	0.304
Interorbital breadth	0.314	−0.060
Breadth of nuchal surface	−0.436	0.995
Biporionic breadth	0.270	−0.651
Basal length	−0.410	1.137
Maximum cranial length	−0.439	−0.366
Palatal length	−0.218	−1.266
Basion to inion	0.070	0.865

In Fig. 2.2, the separation of *G.b. beringei* and *G.b. graueri* is clear, but the four *graueri* samples are somewhat separated. The Tshiaberimu sample – for which the name *rex-pygmaeorum* is available if required – approaches *beringei* and overlaps with it, and the three Kahuzi and four Bwindi specimens (all entered ungrouped) also approach *beringei* somewhat.

In Fig. 2.3, all male skulls are compared, keeping the (now four) presumed subspecies separate. There is a clear separation between *G. gorilla* and *G. beringei*, with just a little overlap; quite unexpectedly, two of the four Bwindi fall within *G. g. gorilla* (this does not mean that they are somehow geographically displaced western gorillas, only that they are different from *beringei* in

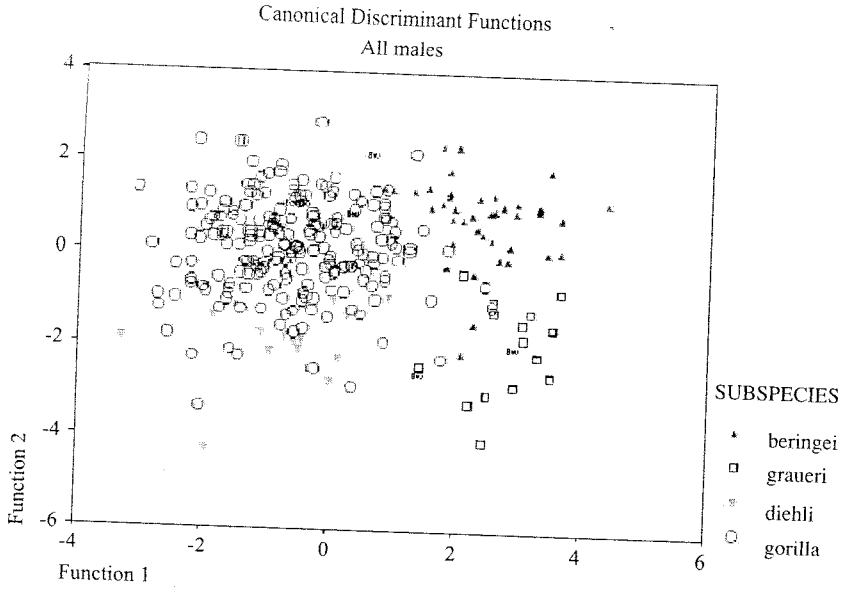

Fig. 2.3. Skulls of the genus *Gorilla*, grouped by subspecies. 19 of the 210 *G. gorilla* skulls (9%, all *G. g. gorilla*) were misclassified as *G. beringei*, but there was no reciprocal misclassification. Within *G. gorilla* only two of the 16 *diehli* skulls (12.5%) are misclassified as *gorilla*; 27 of the 191 gorilla *skulls* (12.9%) are misclassified as *diehli*. Within *G. beringei* only two of the 42 *graueri skulls* (4.8%) are misclassified as *beringei*; one of the 14 *beringei* skulls (7.1%) is misclassified as *graueri*. Bw = Bwindi: the other ungrouped skull (inside the *gorilla* dispersion) is a skull from Bondo. The first discriminant function accounts for 69.7% of the variance, the second for 22.8%. Standardized canonical discriminant function coefficients are as follows:

	Function 1	Function 2
Maximum cranial length	−0.172	0.014
Braincase length	−0.031	−0.054
Palatal breadth at M^1	0.083	0.334
Facial height	−0.176	0.231
Palatal length	1.246	0.125
Interorbital breadth	−0.149	0.442
Breadth of nuchal surface	−0.254	−1.116
Basal length	−0.001	−0.344
Opisthion to inion	0.027	−0.425
Biporionic breadth	−0.156	0.773
Basion to inion	−0.263	0.509

some of the same ways in which *G. gorilla* is). Within each of the species, *graueri* is more distinct from *beringei* than *diehli* is from *gorilla*.

As new methods of investigation become available to us, levels of analysis can be conducted: nuances undreamed of by Wyman, Matschie, Rothschild, even Coolidge. Science has advanced, but human behavior has not. People still hunt gorillas for food or trophies, and still cut down their forests; but now those same advances in science also enable forests to be cut down more efficiently, gorillas to be hunted more efficiently, human populations to increase ever faster and press in on the remaining habitat, so that our second-closest relative is threatened with disappearing for ever. More and more, the work of taxonomists and other biologists must be put at the service of conservation.

References

Alix, E. and Bouvier, A. (1877). Sur un nouvel anthropoïde (*Gorilla mayéma*). *Bulletin de la Société Zoologique de France*, **11**, 2, 488–490.

Anon. (1996). Bwindi's gorillas in the midst of taxonomic dispute. *African Wildlife Update*, Feb. 1996, 7.

Angst, R. (1967). Beitrag zum Formwandel des Craniums der Ponginen. *Zeitschrift für Morphologie und Anthropologie*, **58**, 109–151.

Angst, R. (1970). Über die Schädelkämme der Primaten. *Natur und Museum*, **100**, 293–302.

Angst, R. (1976). Das Endocranialvolumen der Pongiden (Mammalia: Primates). *Beiträge der naturkunliche Forschung in Südwest Deutschland*, **35**, 181–188.

Angst, R. and Storch, G. (1967). Bemerkungen über den Schädel des Gorilla Abraham aus dem Frankfurter zoologischen Garten. *Natur und Museum*, **97**, 417–420.

Bischoff, T.L.W. (1880). Beiträge zur Anatomie des Gorilla. *Abhandlungen des bayerischen Akademie der Wissenschaft*, **13**, 3, 1–48.

Butynski, T., Sarmiento, E.E., and Kalina, J. (1996). More on the Bwindi gorillas. *African Wildlife Update*, Apr. 1996, 6.

Cave, A.J.E. (1959). The nasal fossa of a foetal gorilla. *Proceedings of the Zoological Society of London*, **133**, 73–77.

Cave, A.J.E. 1961. The frontal sinus of the gorilla. *Proceedings of the Zoological Society of London*, **136**, 359–373.

Colyer, F. (1936). *Variations and Diseases of the Teeth of Animals*. London: John Bale & Sons.

Coolidge, H.J. (1929). A revision of the genus *Gorilla*. *Memoirs of the Museum of Comparative Zoology, Harvard*, **50**, 291–381.

Coolidge, H.J. (1936). Zoological results of the George Vanderbilt African Expedition of 1934. IV: Notes on four gorillas from the Sanga River region. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **88**, 479–501.

Corbet, G.B. (1967). Nomenclature of the "Eastern Lowland Gorilla". *Nature*, **215**, 1171–1172.

Cousins, D. (1974). Classification of captive gorillas *Gorilla gorilla*. *International Zoo Yearbook*, **14**, 155–159.

Duckworth, W.L.H. (1915). *Morphology and Anthropology*. Cambridge, U.K.: Cambridge University Press.

Elliot, D.G. (1913). *Review of the Primates*. New York: American Museum of Natural History.

Famelart, L. (1883). Observations sur un jeune gorille. *Bulletin de la Société Zoologique de France*, **8**, 149–152.
Frechkop, S. (1943). *Exploration du Parc National Albert, Mission S. Frechkop (1937–8)*. Brussels: Institut des Parcs Nationaux du Congo Belge.
Fritze, A. (1912). Kleinere Mitteilungen. I: *Gorilla gorilla* Schwarzi Matschie. *Jahrbuch der Provinzialmuseum, Hannover*, **1912**, 113.
Garner, K.J. and Ryder, O.A. (1996). Mitochondrial DNA diversity in gorillas. *Molecular Phylogenetics and Evolution*, **6**, 39–48.
Geoffroy St. Hilaire, I. (1852). Sur les rapports naturels du gorille: Remarques faites à la suite de la lecture de M. Duvernoy. *Comptes rendus de l'Académie des Sciences, Paris*, **36**, 933–936.
Geoffroy St. Hilaire, I. (1855). Description des mammifères nouveaux ou imparfaitement connus de la collection du Muséum d'Histoire Naturelle et remarques sur la classification et les caractères des mammifères. *Archives du Muséum d'Histoire Naturelle, Paris*, **10**, 1–102.
Gregory, W.K. (ed.) (1950). *The Anatomy of the Gorilla*. New York: Columbia University Press.
Groves, C.P. (1967). Ecology and taxonomy of the gorilla. *Nature*, **213**, 890–893.
Groves, C.P. (1970). Population systematics of the gorilla. *Journal of Zoology, London*, **161**, 287–300.
Groves, C.P. (1985). The case of the pygmy gorilla: A cautionary tale for cryptozoology. *Cryptozoology*, **4**, 37–44.
Groves, C.P. (1998). Of course the Giant Sable is a valid subspecies. *Gnusletter*, **17**, 1, 4.
Groves, C.P. (2000). What, if anything, is taxonomy? *Gorilla Journal*, **21**, 12–15.
Groves, C.P. (2001). *Primate Taxonomy*. Washington, D.C.: Smithsonian Institution Press.
Groves, C.P. and Humphrey, N.K. (1973). Asymmetry in gorilla skulls: Evidence of lateralized brain function? *Nature*, **244**, 53–54.
Groves, C.P. and Stott, K.W., Jr. (1979). Systematic relationships of gorillas from Kahuzi, Tshiaberimu and Kayonza. *Folia Primatologica*, **32**, 161–179.
Haddow, A.J. and Ross, R.W. (1951). A critical review of Coolidge's measurements of gorilla skulls. *Proceedings of the Zoological Society of London*, **121**, 43–54.
Hartmann, R. (1886). *Anthropoid Apes*. New York: Appleton & Co.
Haeckel, E. (1903). *Anthropogenie*, 5th edn, vol. 1, *Keimesgeschichte des Menschen*. Leipzig: Engelmann.
Heuvelmans, B. (1981). *Les Bêtes Humaines d'Afrique*. Paris: Pion.
Huxley, T.H. (1867). On the zoological relations of Man with the lower animals. *Natural History Review*, 1867, **1**, 67–84.
International Code of Zoological Nomenclature, 4th edn, adopted by the XX General Assembly of the International Union of Biological Sciences. London: International Trust for Zoological Nomenclature, in association with British Museum (Natural History).
Keith, A. (1896). An introduction to the study of the anthropoid apes. I: The gorilla. *Nature and Science*, **9**, 26–37.
Lönnberg, E. (1917). Mammals collected in Central Africa by Captain E. Arrhenius. *Proceeding, Kunglisk Svenska Vetensk-Akademisk Handlingar*, **58**, 2, 1–110.
Lovell, N.C. (1990). Skeletal dental pathology of free-ranging mountain gorillas. *American Journal of Physical Anthropology*, **81**, 399–412.
Maly, J. (1939). Kostra ranèné gorily. *Anthropologie*, **17**, 21–36.
Matschie, P. (1903). Über einen Gorilla aus Deutsch-Ostafrika. *Sitzungsberichte des Gesellschaft naturforschender Freunde, Berlin*, **1903**, 253–259.
Matschie, P. (1904). Bemerkungen über die Gattung *Gorilla*. *Sitzungsberichte des Gesellschaft naturforschender Freunde, Berlin*, **1904**, 45–53.
Matschie, P. (1905). Merkwürdige Gorilla-Schädel aus Kamerun. *Sitzungsberichte des Gesellschaft naturforschender Freunde, Berlin*, **1905**, 277–283.
Matschie, P. (1914). Neue Affen aus Mittelafrika. *Sitzungsberichte des Gesellschaft naturforschender Freunde, Berlin*, **1914**, 323–342.
Miller, G.S. (1915). The jaw of the Piltdown Man. *Smithsonian Miscellaneous Collections*, **65**, 12, 7–31.
Neuville, H. (1916). Remarques sur la variabilité de la crête sagittale de crane des gorilles. *Bulletin du Muséum d'Histoire Naturelle, Paris*, **22**, 2–7.
Neuville, H. (1932). La classification des gorilles. *L'Anthropologie*, **42**, 330–337.
Owen, R. (1848*a*). On a new species of chimpanzee (*T. savagei*). *Proceedings of the Zoological Society of London*, **1848**, 27–35.
Owen, R. (1848*b*). Supplementary note on the great chimpanzee (*Troglodytes gorilla, Trogl. savagei* Owen). *Proceedings of the Zoological Society of London*, **1848**, 53–56.
Owen, R. (1848*c*). Osteological contributions to the natural history of the chimpanzees (*Troglodytes*, Geoffroy) including the description of the skull of a large species (*Troglodytes gorilla*, Savage) discovered by Thomas Savage, M.D., in the Gabon country, West Africa. *Transactions of the Zoological Society of London*, **3**, 381–422.
Owen, R. (1857). On the characters, principles of division and primary groups of the class Mammalia. *Proceedings of the Linnean Society*, **1857**, 2, 1–37.
Owen, R. (1861). On the cerebral characters of Man and the ape. *Annals and Magazine of Natural History*, **7**, 3, 456–458.
Owen, R. (1862*a*). Osteological contributions to the natural history of the chimpanzees (*Troglodytes*) and orangs (*Pithecus*). IV: Description of the cranium of an adult male gorilla from the River Danger, West coast of Africa, indicative of a variety of the Great Chimpanzee (*Troglodytes gorilla*), with remarks on the capacity of the cranium and other characters shown by sections of the skull, in the orangs (*Pithecus*), chimpanzees (*Troglodytes*), and in different varieties of the human race. *Transactions of the Zoological Society of London*, **4**, 75–88.
Owen, R. (1862*b*). Osteological contributions to the natural history of the chimpanzees (*Troglodytes*) and orangs (*Pithecus*). V: Comparison of the lower jaw and vertebral column of the *Troglodytes gorilla, Troglodytes niger, Pithecus satyrus*, and in different varieties of the human race. *Transactions of the Zoological Society of London*, **4**, 89–116.
Rothschild, W. (1905). Notes on anthropoid apes. *Proceedings of the Zoological Society of London*, **1905**, **2**, 413–440.

Rothschild, W. (1908). Note on *Gorilla gorilla diehli* (Matschie). *Novitates Zoologicae*, **15**, 391–392.
Rothschild, W. (1927). On a new race of Bongo and of Gorilla. *Annals and Magazine of Natural History*, **19**, 9, 271.
Ruvolo, M., Pan, D., Zehr, S., Goldberg, T., Disotell, T.R., and von Dornum, M. (1994). Gene trees and hominoid phylogeny. *Proceedings of the National Academy of Sciences U.S.A.*, **91**, 8900–8904.
Rzasnicki, A. (1936). Versuch einer Rassenunteilung der Gorillas. *Annales Musei Zoologici Polonici*, **15**, 11, 1–32.
Sarmiento, E.E. (1994). Terrestrial traits in the hands and feet of gorillas. *American Museum Novitates*, **3091**, 1–56.
Sarmiento, E.E., Butynski, T.M., and Kalina, J. (1996). Gorillas of Bwindi-Impenetrable Forest and the Virunga Volcanoes: Taxonomic implications of morphological and ecological differences. *American Journal of Primatology*, **40**, 1–21.
Savage, T.S. and Wyman, J. (1847). Notice of the external characters and habits of *Troglodytes gorilla*, a new species of orang from the Gaboon River; Osteology of the same. *Boston Journal of Natural History*, **5**, 417–442.
Schaller, G.B. (1963). *The Mountain Gorilla: Ecology and Behavior*. Chicago, IL: University of Chicago Press.
Schultz, A.H. (1934). Some distinguishing characters of the mountain gorilla. *Journal of Mammalogy*, **15**, 51–61.
Schultz, A.H. (1962). Die Schädelkapazität männlicher Gorillas und ihr Höchstwert. *Anthropologischer Anzeiger*, **25**, 197–203.
Schwarz, E. (1927). Un gorille nouveau de la forêt de l'Ituri, *Gorilla gorilla rex-pygmaeorum* subsp. n. *Revue de Zoologie et Botanique Africaine*, **14**, 333–336.
Schwarz, E. (1928). Die Sammlung afrikanischer Affen in Congo-Museum. *Revue de Zoologie et Botanique Africaine*, **16**, 2, 1–48.
Slack, J.H. (1862). Note on *Gorilla castaneiceps*. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **1862**, 159–160.
Sonntag, C.F. (1924). *The Morphology and Evolution of the Apes and Man*. London: John Bale, Sons & Danielson.
Stumpf, R.M., Fleagle, J.G., Jungers, W.L., Oates, J.F., and Groves, C.P. (1998). Morphological distinctiveness of Nigerian gorilla crania. *American Journal of Physical Anthropology Supplement*, **1998**, 213.
Vogel, C. (1961). Zur systematischen Untergliederung der Gattung *Gorilla* anhand von Untersuchungen der Mandibel. *Zeitschrift für Säugetierkunde*, **26**, 2, 1–12.
Wilson, L.G. (1996). The gorilla and the question of human origins: The brain controversy. *Journal of the History of Medicine and Allied Sciences*, **51**, 184–207.
Wyman, J. (1847). A communication from Dr. Thomas S. Savage, describing the external character and habits of a new species of *Troglodytes* (*T. gorilla*, Savage,) recently discovered by Dr. S. in Empongwe, near the river Gaboon, Africa. *Proceedings of the Boston Society of Natural History*, **2**, 245–7.

3 *Patterns of diversity in gorilla cranial morphology*

REBECCA M. STUMPF, JOHN D. POLK, JOHN F. OATES, WILLIAM L. JUNGERS, CHRISTOPHER P. HEESY, COLIN P. GROVES, AND JOHN G. FLEAGLE

Introduction

Gorillas, perhaps because of their size, always seem to be the subject of spectacularly divergent interpretations. Views of their behavior have ranged from the rapacious, vicious giant ape of the nineteenth century, through Robert Ardrey's (1961) view of them as lethargic, depressed, evolutionary dead ends, to the current view of them as gentle giants, albeit with infanticidal tendencies. Views of gorilla systematics have been no less diverse over the past century and a half (see review by Groves, this volume). Beginning with the initial description of *Gorilla gorilla* by Savage and Wyman in 1847 through the 1920s, ten separate species of *Gorilla* were described by systematists from all over the world, often from a single skull. The modern systematics of *Gorilla* stems from the work of Harold Jefferson Coolidge in 1929. Coolidge reviewed all of the previously described species and provided measurements and graphs of 213 specimens from seven major geographic regions. He placed all gorillas in a single species, *Gorilla gorilla*, in accordance with others such as Rothschild (1906), Elliot (1913), and Schwarz (1928), but went even further in identifying only two subspecies – *Gorilla gorilla gorilla* for the gorillas of western and central Africa, and *Gorilla gorilla beringei* for gorillas from the Virunga mountains and adjacent regions.

More recently, *Gorilla* systematics has derived almost exclusively from Groves's (1970, 1986; also Groves and Stott, 1979) study of 747 skulls and over 100 skeletons. Groves largely followed Coolidge (1929) in recognizing a single species, but recognized three subspecies: *Gorilla gorilla gorilla*, the western lowland gorilla; *G. g. beringei*, the mountain gorilla from the Virunga volcanos; and *G. g. graueri*, the eastern lowland gorilla from "the Eastern Congo lowlands and the mountains to the west of Lakes Tanganyika and Edward" (Groves, 1970:298). Subsequently, there have been various questions concerning the relationships among eastern gorillas. Are the eastern lowland gorillas (*G. g. graueri*) more closely related to western lowland gorillas (*G. g. gorilla*)